

Negative Effects of *Azteca* Ants on the Distribution of the Termite *Neocapritermes braziliensis* in Central Amazonia

by

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ABSTRACT

Termites play important roles in tropical ecosystem functioning, and their evolutionary success has been linked to their defense mechanisms. However, microhabitat overlap with potential aggressors may constrain their distribution and thus, their environmental impacts on an ecological timescale. We investigated a possible negative effect of abundant generalist ants (*Azteca* sp.) on the termite *Neocapritermes braziliensis*. Both taxa frequently build their nests attached to trees. We determined the densities of their active nests in 10 plots (250 x 10 m) systematically distributed over 5 km² in central Amazonia, Brazil, and recorded their co-occurrence in individual trees. Using generalized nonlinear modeling in a Bayesian framework, we found good support for a negative effect of *Azteca*'s nest density on *N. braziliensis*'s. This effect conformed to a power law, and accounted for more than half of the variation in the termite's nest density ($r^2 = 0.56$). Additionally, of all counted *N. braziliensis* mounds, only 1.08 percent was attached to trees also hosting *Azteca*. Such patterns may have arisen due to *N. braziliensis*'s inability to establish new nests within *Azteca* territories, or predation by ants on established colonies of the termite. We suggest that even non-strictly termitophagous ant species may have important impacts on termite populations and, consequently, on their roles in nutrient cycling and ecosystem engineering.

Key Words: Bayesian inference; generalized nonlinear modeling; population limitation; power law; social insect; species distribution.

INTRODUCTION

Population size is subject to different constraints, which is the basis for spatial variation in species abundance (Krebs 2002). There has been a long

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debate on whether populations are mainly driven by bottom-up (resources) or top-down forces (predation) (Hairston *et al.* 1960; Hunter & Price 1992; Polis & Strong 1996; Borer *et al.* 2006). It has been recently argued that under most circumstances animal populations are limited by food quality or quantity (White 2008). However, while resource availability may set an upper limit to prey populations, predation may prevent these populations from reaching carrying capacity (McIntosh *et al.* 2005), especially under the presence of generalist predators (Jiang & Morin 2005). This might be reinforced when a predator is both generalist and more abundant than a particular prey, so that the predator may limit this prey's populations without being limited in turn. Nonetheless, it is likely that any such effect depends on the spatial scale under consideration (Levin 1992).

Ants (Hymenoptera: Formicidae) and termites (Blattaria: Isoptera) are well known for their convergent social evolution, but they are also closely connected by trophic interactions. In fact, ants are generally more abundant than termites and, although few ant species are strictly termitophagous, most ants prey upon termites if allowed to (Hölldobler & Wilson 1990). This, coupled with the diverse array of termite defense strategies, has been taken as evidence for an evolutionary arms race between both taxa (Noirot & Darlington 2000). Nevertheless, current ant-termite interactions remain poorly explored, especially in tropical rainforests, where they are remarkably abundant and diverse (Scholtz *et al.* 2008). Given the acknowledged roles of social insects in the functioning of these ecosystems, understanding interactions between these groups can contribute to the conservation of the environmental services they provide (Chapman & Bourke 2001).

In the Amazon rainforest, nests of several ant and termite species are conspicuous. Namely, arboreal ants of the genus *Azteca* (Formicidae: Dolichoderinae) are dominant in some areas. They build large carton, stalactite-like nests on trees and attend coccid hemipterans for honeydew (Blüthgen *et al.* 2000), although they can be predatory too (Dejean *et al.* 2009). Similarly, *Neocapritermes braziliensis* (Termitidae: Termitinae) is a common, although poorly studied, mound-building termite from the same areas. It feeds on rotting wood, and its mounds are often attached to the base of tree trunks (Constantino 1992). Therefore, encounters between *N. braziliensis* and *Azteca* are likely.

Being a cryptic forager, *N. braziliensis* should be inaccessible to predators most of the time and the combination between cryptic behavior and the physical structure of the mound may allow the termite to avoid predation by ants (Buczkowski & Bennett 2008). However, termite nests are potential targets for predation because they represent concentrated food resources. Also, *Neocapritermes* species have rather low soldier/worker ratios (around 1:100; Krishna & Araujo 1968), a trait likely to affect termite susceptibility to predation by ants (Wells & Henderson 1993).

Because *Azteca* and *N. braziliensis* overlap in their nest substrates and can be locally abundant, their point interactions may result in agonistic patterns at larger scales. Here, we investigate whether *N. braziliensis* and *Azteca* are negatively associated at the levels of individual trees and nest densities across the landscape.

MATERIAL AND METHODS

The study was undertaken in a lowland rainforest area of 10 km² between the Purus and Madeira rivers, Amazonas State, Brazil (3°41'9.85"S, 60°19'9.65" W). Local topography is weakly undulated, and much of the substrate is waterlogged in the wet season.

Fieldwork was carried out from May to June 2009. We surveyed ten plots of 250 x 10 m, distributed along two parallel 5-km trails 1 km apart from each other; both trails contained five sampling plots also 1 km apart from each other. Plots were oriented along topographic contour lines so as to reduce soil variation (as well as its correlates) within sampling units, thus maximizing between-plot variation (Costa & Magnusson 2010).

In each plot, we counted active nests of both taxa, which were recognized by their typical architecture and residents. We also recorded whether each nest co-occurred with a nest of other taxon in the same substrate. Samples were taken for taxonomic confirmation and deposited in the Entomological Collection of the National Institute for Amazonia Research (INPA), Manaus, Brazil. Since all surveyed ants were equivalent in terms of their nesting and foraging modes, they were pooled for analysis.

Following graphical inspection of the data, we modeled *N. braziliensis* nest density (Y) as a power function of *Azteca* nest density (X), assuming a log link (i.e. $\log(Y) = \beta_0 \cdot X^{\beta_1}$) and Poisson distributed errors given the count

response. The model was fit in a Bayesian framework, which allows direct probabilistic statements about parameters and produces exact results even for small sample sizes (Link & Barker 2010). We used uninformative priors (normally distributed with zero mean and standard deviation of 1000) so that inference was mainly driven by the data themselves (i.e. likelihood). Three parallel Markov Chain Monte Carlo simulations (MCMC) were iterated 300,000 times each using the Gibbs sampler, starting from random values and with a thinning rate of 10. The first 1000 realizations of each chain were discarded as burn-in. Chain convergence was checked with trace plots, autocorrelation plots and the Brooks-Rubin-Gelman statistic (BRG). Once validated, chains were pooled for inference ($n = 89,700$), and the means of the resulting posterior distributions were used as point estimates for model parameters. We assessed model adequacy by plotting residuals against fitted values and by squaring the correlation between model predictions and the observed response (r^2) (Zheng & Agresti 2000). We refrained from formal inference regarding nest substrate overlap since our sample was biased towards the presence of nests.

Modeling was carried out in R 2.10.1 (R Core Development Team 2009) coupled to WinBUGS 1.4 (Spiegelhalter *et al.* 2003), with the R package "R2WinBUGS" (Sturtz *et al.* 2005) as interface between the two programs.

RESULTS

We counted 30 nests of *Azteca* and 54 of *N. braziliensis*. These values correspond to local densities of 12 nests/ha and 21.6 nests/ha, respectively. The model for the relation between nest densities was fit as $\log(Y) = 2.35 \cdot X^{-0.49}$ (Fig. 1) and accounted for more than half the variation in the response ($r^2 = 0.56$). MCMC diagnostics indicated chain convergence (BRG = 1) and no autocorrelation, whereas residual analysis revealed no clear patterns, thus validating the model. The 95% credible interval (i.e. within which there is a 95% chance the true parameter value is found) for the constant β_0 ranged from 1.98 to 2.69, and from -0.25 to -0.76 for the exponent β_1 . Also, only two nests of *N. braziliensis* (1.08% of this species' total) were attached to trees hosting *Azteca* nests.

DISCUSSION

This study provides evidence that arboreal *Azteca* ants act as limiting factors of *N. braziliensis* in the study area. Not only nests appear to strongly segregate among substrate trees, but there is also a negative, nonlinear relationship between nest densities across the landscape. Presumably, these patterns emerge from ant-termite behavioral interactions at the level of individuals. Hence the observed patterns suggest a scalable negative effect. We did not observe aggression by *Azteca* against undisturbed termites during the present study, though we did observe the ants attacking both *N. braziliensis* workers and soldiers that were removed from their nests.

Impacts of ants on termites have been recorded several times in the field. For instance, Jutsum *et al.* (1981) detected a negative association between

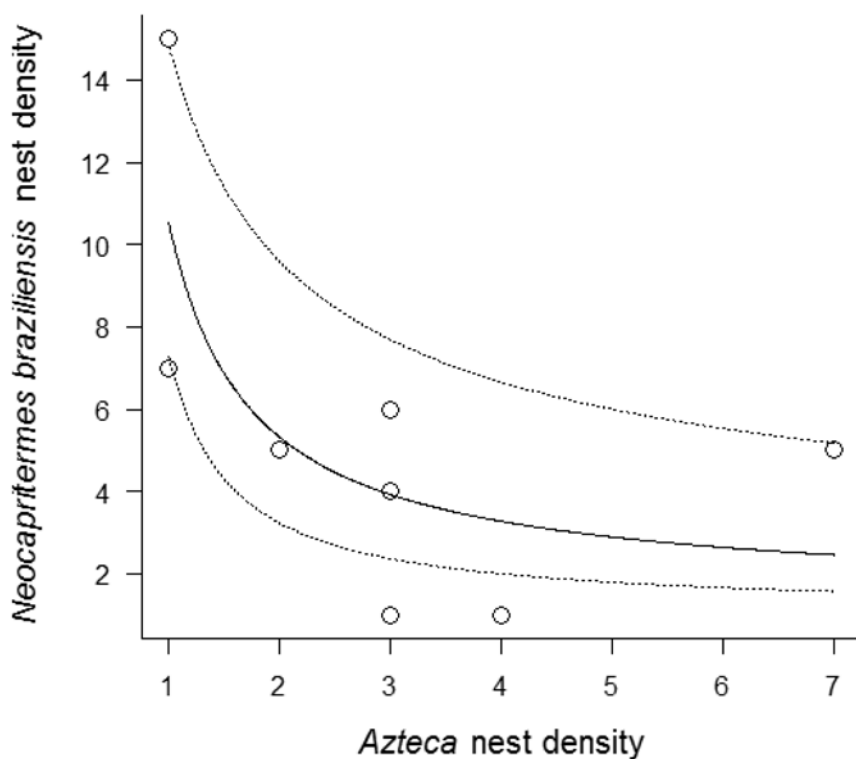


Fig. 1. Mean response (solid line) of *Neocapritermes braziliensis*' nest density to *Azteca*'s, estimated as $\log(Y) = 2.35 \cdot X^{-0.49}$. Dotted lines are 95% credible limits.

the presence of *Azteca* sp. and *Nasutitermes corniger* (*syn. N. costalis*) on trees in Trinidad; Leponce *et al.* (1999) argued that the presence of the ant *Crematogaster irritabilis* was a limiting factor for arboreal termites in New Guinea, causing a two-fold decrease in their local abundance; Gonçalves *et al.* (2005) recorded a strong negative effect of predatory ants on arboreal termite activity; and Dejean *et al.* (2007a) found that the nest densities of arboreal *Nasutitermes* were about three times lower in plots occupied by the invasive ant *Pheidole megacephala* than in those ones without this species.

We note, however, that *Azteca* has neither the morphological nor behavioral traits known from specialized, termite-hunting species (e.g. Leal & Oliveira 1995). Thus, it is improbable that it normally raids termite nests. Nonetheless, most ant taxa are known to prey on exposed termites in central Amazonia (Bandeira 1979), and our results suggest that even ant species that do not specialize in termitophagy (such as *Azteca* spp.) may have strong negative effects on natural termite populations. The fact that this observation involves a termite species presumably well protected by the mound structure such as *N. braziliensis*, somewhat contradicts previous suggestions (Mill 1982; Buczkowski & Bennett 2008).

We propose two hypotheses to account for the observed patterns. *Azteca* could affect *N. braziliensis* populations by inhibiting newly mated reproductive pairs from founding new colonies within its territories. Different colonies of the same termite species can liberate their alates in synchronized events, and these attract many opportunist predators – including ants (Mill 1983). In this scenario, *Azteca* would prey upon *N. braziliensis* only sporadically, due to random encounters during swarming. This would suffice to produce segregation between nesting substrates. If the probability of encounters were a function of nest density, then higher densities of *Azteca* nests would also reduce *N. braziliensis*' nest founding success and thus, the termite's nest densities themselves.

Our second hypothesis is that *Azteca* could shift its foraging at least partially towards termites if they become locally abundant. Arboreal ants exhibit strong preference for protein-rich baits in comparison to litter-dwelling ones, suggesting that their colonies are limited by nitrogen availability (Kaspari & Yanoviak 2001). Thus, *Azteca* may take advantage of the protein supply represented by *N. braziliensis* colonies. Termite mounds can be cracked by rainfall,

tree fall or specialized predators (e.g. anteaters, armadillos, nest-raiding ants), which may allow generalist ants to raid nests. These two hypotheses are not mutually exclusive, though.

Why would *N. braziliensis* nest density relationship with *Azteca*'s follow a negative power function? Ants are territorial insects and thus are expected to compete for space (Parr & Gibb 2010). For instance, experimental work has revealed that higher nest densities intensify intraspecific conflict in the fire ant *Solenopsis invicta* (Adams & Tschinkel 2001). Accordingly, a shift in the strength of interactions from inter- to intraspecific ones as ant nest density increases may dampen the predatory impact of ants on termites and thus, the rate of decline in termite abundance.

Dominant arboreal ants engage in the defense of well-marked territories against conspecifics as well as other ant species, which can lead to the establishment of unoccupied zones or "no ant's lands" between adjacent, competing colonies (Dejean *et al.* 2007b). Hence it may also be that these areas provide termites with refuges from the ant "crossfire" (e.g. by going unnoticed during earlier, more vulnerable stages of colony development). In addition, dominant ant species only have absolute control of the immediate nest neighborhood; there is plenty of within-territory space for opportunistic foraging (Andersen 2008) and, perhaps, termite nest founding and growth.

The present study suggests a role for non-strictly termitophagous ants as effective limiting factors of natural termite populations at multiple scales. It has been observed that temporal gaps in termite activity can be a function of predation risk by ants (Korb & Linsenmair 2002; DeSouza *et al.* 2009). Thus, the limiting effects of ants on termite populations may further impair termite roles in ecosystem functioning such as nutrient cycling and ecosystem engineering. However, further study of the mechanisms creating the observed patterns is necessary. We encourage the application of Bayesian inference in future studies, as they could build on informative priors (i.e. posterior distributions as estimated here) to strengthen the robustness of their conclusions (McCarthy & Masters 2005).

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